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Evidence for color and luminance invariance of global form mechanisms

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Human visual cortex contains mechanisms that pool local orientation information over large areas of visual space to support percepts of global form. Initial studies concluded that some of these mechanisms are cue invariant, in that they yield form percepts irrespective of whether the visual signals contain luminance or chromatic information. Later studies reported that these mechanisms are chromatically selective, albeit with a broad tuning in color space. We used Glass patterns and the phenomenon of adaptation to determine whether Glass pattern perception is mediated by mechanisms that are color and/or luminance selective, or not. Subjects were adapted to either a radial or concentric Glass pattern of a given color or luminance polarity. We measured the effect of adaptation on subsequent detection of Glass patterns with the same or different visual attributes. Our results show that adapting to a concentric or radial pattern significantly elevates threshold for the subsequent detection of patterns of the same form, irrespective of their color or luminance polarity, but that adaptation to luminance leads to higher threshold elevations than adaptation to color. We conclude that Glass pattern perception is mediated by perceptual mechanisms that are color invariant but not totally insensitive to the difference between color and luminance information.

Keywords: Glass patterns, color vision, form vision, human psychophysics

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Introduction

Understanding how the visual system treats the different attributes of a scene has been one of the major challenges of visual neuroscience. In this study, we examined the effect of color and luminance on form perception. To address this problem, we used Glass patterns (Glass, 1969).

Glass patterns have been used extensively in psychophysical (Dakin, 1997; Dakin & Bex, 2001, 2002; DeValois & Switkes, 1980; Glass & Switkes, 1976; Kovacs & Julesz, 1992; Wilson & Wilkinson 1998; Wilson, Wilkinson, & Asaad, 1997) and physiological (Smith, Bair, & Movshon, 2002; Smith, Kohn, & Movshon, 2007) studies for the investigation of form detecting mechanisms. These stimuli are made by superimposing two identically distributed random dot patterns after geometrically transforming one of them. Depending on the geometrical rule used, Glass patterns can elicit the perception of different forms. For instance, if the pairs' orientation is perpendicular with respect to a radial line projecting from the center of the stimulus, a concentric Glass pattern is formed, and if the orientation is an extension of the radial line, a radial Glass pattern is formed.

Several studies have suggested that the processing of Glass patterns happens in two stages: a local and a global one (Smith et al., 2002; Wilson & Wilkinson, 1998; Wilson, Switkes, & DeValois, 2004). The first stage identifies the local orientation cues (dot pairs); the second integrates these cues to reveal a global structure. Wilson and Wilkinson (1998) proposed a neural model for Glass pattern detection in which the signal is passed through an oriented filter, then rectified and passed to a second oriented filter with a larger receptive field. The outputs of this process are finally pooled and summed. Dickinson and Badcock (2007) used a summation near threshold protocol to show that global structure perception can be explained by just four such pooling stages, including one specialized for radial and one for concentric patterns.

Modeling studies hypothesized that the initial oriented filtering occurs in V1, the rectification and second oriented filtering in V2, and the final pooling stage in V4. Subsequent electrophysiological studies on macaque monkeys (Smith et al., 2002, 2007) have indicated that indeed V1 and V2 neurons process the local orientation cues in Glass patterns.

Previous studies that used colored Glass patterns to examine the interaction between color and form processes drew conflicting conclusions. Cardinal and Kiper (2003) and Mandelli and Kiper (2005) argued that both local and global stages of form processing are color selective, with global form mechanisms being more broadly tuned than local ones. On the other hand, Wilson and Switkes (2005; see also Kovacs & Julesz, 1992) concluded that only the

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local stage of form processing is color selective, and that the global stage is mediated either by complex cells that show no color selectivity or by a mechanism that combines inputs from color-selective cells.

In this study, we use adaptation to probe the chromatic and achromatic (luminance) properties of the global form-selective mechanisms. Adaptation is a powerful tool for the investigation of the mechanisms responsible for the processing of specific stimuli (Graham, 1989). Clifford and Weston (2005) showed that adaptation to a Glass pattern causes a significant increase in threshold for the subsequent detection of patterns of the same type. This adaptation effect even leads a random pattern to appear concentric after adaptation to a radial pattern, and vice versa.

Our results indicate that global form mechanisms are both luminance and color invariant. In our first experiment, we show that adaptation to a Glass pattern defined by color (without any luminance information) increases the coherence thresholds for the detection of a subsequent Glass pattern of the same form, irrespective of its color. We also used Glass patterns that contained solely achromatic dots and obtained the same effect as in our first experiment: only form determines the magnitude of adaptation. Our study strongly suggests that global form mechanisms combine inputs from color- and luminance-selective cells.

Methods

Subjects

Thirteen subjects (six females) aged 23 to 46 participated in the experiments. All subjects had previously obtained normal scores in the Ishihara color test and had normal or corrected-to-normal vision. The two authors participated in all experiments. At least three subjects were tested for each adapting condition. All procedures conformed to the Declaration of Helsinki.

Stimuli

Stimuli were displayed on a gamma-corrected Sony G200P monitor driven by a ViSaGe (Cambridge Research Systems, UK) graphics board (spatial resolution of 800 × 600 pixels, refresh rate of 100 Hz). The subjects' head rested on a chin rest positioned 50 cm from the monitor. In all experiments, the only source of light came from the monitor.

DKL color space

Stimuli were represented in the three-dimensional DKL color space (Derrington, Krauskopf, & Lennie, 1984). This physiologically based coordinate system is defined by two axes in which only chromaticity varies and an axis orthogonal to them where luminance varies but chromaticity is fixed. Along one axis of the chromaticity plane, the signal from short-wavelength (S)-sensitive cones does not change but the signal from long-wavelength (L)- and middle-wavelength (M)-sensitive cones co-vary so that their sum remains constant. This axis is loosely called the Red–Green, or R–G axis. Along the other chromaticity axis (S–(L + M), or Blue–Yellow (B–Y) axis), the signal from the S cones varies while the signal from the L and M cones stays fixed. Along the luminance axis, signals from all three cones vary proportionally. At the point of intersection of the three axes is a white point.

A point in the DKL color space can be represented by three parameters: its *azimuth*, which is defined as the angle that is formed between the projection of the point to the isoluminant plane and the R–G axis; its *elevation*, which is the angle that is formed between the point and its projection onto the isoluminant plane; and its *amplitude*, which is the length of the vector that starts from the white point and ends at the point of interest.

In this study, we define 0 deg azimuth as red, 90 deg azimuth as yellow, 180 deg azimuth as green, and 270 deg azimuth as blue.

Glass patterns

Glass pattern stimuli consisted of 200 randomly positioned dot pairs. The diameter of the dots was 22 min and the distance between the dot pairs was 34.5 min. We used large dot sizes to minimize luminance artifacts induced by chromatic aberrations. All stimuli were presented on a gray background with luminance of 28 cd/m^2. At the viewing distance we used, the screen subtended 32 by 42 deg of visual angle, and Glass patterns subtended 20 deg of visual angle. All colored Glass patterns were photometrically isoluminant with the background. We opted to not measure all individual subjects' isoluminant point since our stimulus size is large and the isoluminant point varies with eccentricity (Bilodeau & Faubert, 1997). Luminance-defined Glass patterns varied in luminance but not in chromaticity with the background. The fixation point was a white circle located in the center of the screen subtending 31.5 min.

Perceptual isoluminance

To ensure that possible individual deviations from photometric isoluminance did not affect our results, we measured perceptual isoluminance for two of our subjects, who thus performed the same experiments both at photometric and perceptual isoluminances. Perceptual isoluminance was measured using heterochromatic flicker photometry. Subjects had to null the flicker of a foveally presented disk sinusoidally flickering at 30 Hz. The disk alternated between two colors presented on an equiluminant gray background. We measured perceptual isoluminance

between all colors subsequently used in the experiments and the neutral gray background at the origin of DKL space.

Each isoluminant pair was measured three times by the method of adjustments. Subjects adjusted the luminance of one of the two colors until flicker was nulled. The average of the three final settings was used for each color in subsequent experiments.

For the experiments performed at perceptual isoluminance, we also reduced the Glass pattern size to 10 deg, a range of eccentricity within which variations of the perceptual isoluminant point is minimal (Bilodeau & Faubert, 1997). We reduced the total number of dot pairs to 90. In one subject, we also scaled the dot size (16 min) and interdot distance (26 min).

Experimental procedure

The following procedure applies to all psychophysical experiments, except for the preliminary and baseline ones (see below). Subjects were exposed to an initial adaptation that lasted 2 min. Each trial was then preceded by a top-up adaptation of 5 s. To minimize local adaptation, the adapting stimulus was updated with a new set of coordinate pairs every 500 ms. The adapting stimulus characteristics (form, color) did not change throughout a session.

We used a two-interval forced-choice procedure for all our experiments. Two successive test stimulus presentations started 250 ms after the presentation of the top-up adapting stimuli. Each of the stimuli was presented for 250 ms, separated by a 250-ms interval. One of the intervals contained either a radial or a concentric Glass pattern, the other an array of randomly oriented dot pairs. Both intervals were preceded by a brief sound cue. Subjects had to indicate with two button presses in which of the two intervals the Glass pattern was presented and whether the pattern was radial or concentric. Each button press was followed by a feedback tone indicating whether the response was correct or not. Figure 1 illustrates a representative trial.

If both button presses were correct, the response was considered correct. We used a staircase protocol to obtain the subjects' coherence thresholds for the perception of concentric and radial Glass patterns. Coherence is defined as the percentage of dot pairs oriented properly to define the desired pattern, the remaining dot pairs being given a random orientation. After three consecutive correct responses, the coherence of the pattern was decreased by a fraction of a log unit; after an incorrect response, the coherence of the pattern was increased by the same amount. For the first five staircase reversals, the fraction was 0.5; thenceforth, it switched to 0.1. Each staircase stopped after eleven reversals. The threshold was calculated as the average of the last seven reversal values.

Experiments

In DKL space, the scaling of the axes is arbitrary. We chose to scale the axes by measuring the subjects'

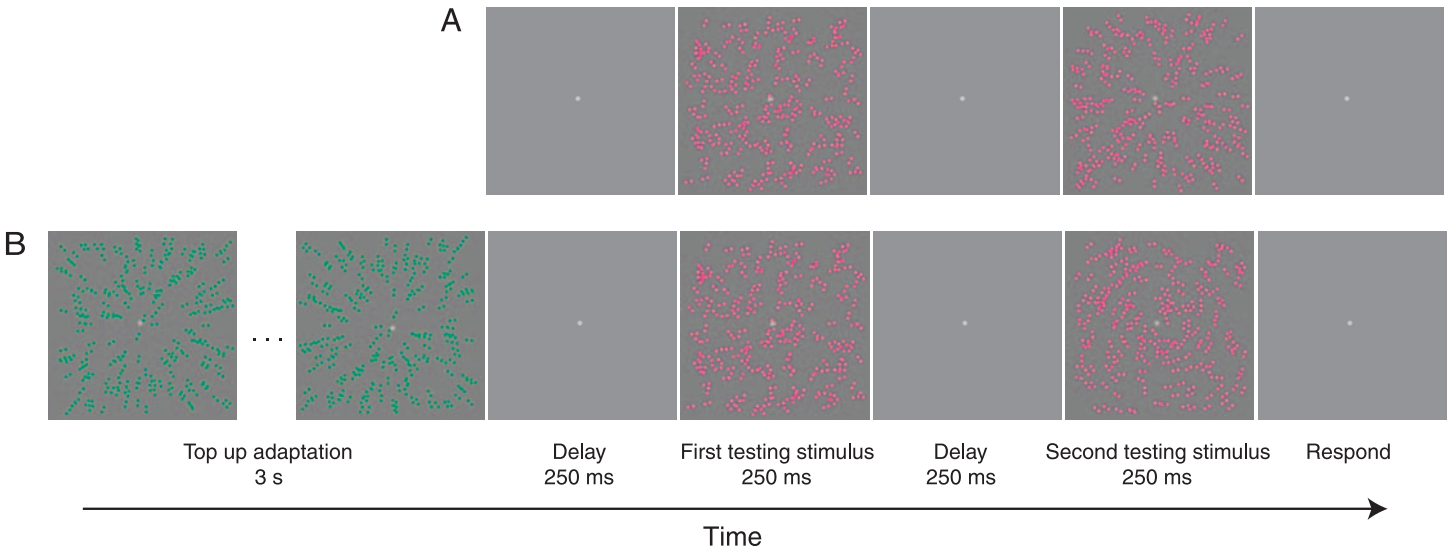


Figure 1. Schematic representation of a trial in each of the different experiments. We have added luminance contrast in the figure to make the dots more visible. (A) Baseline experiment: in each trial, subjects were shown two sequential stimuli. Stimuli and the delay lasted 250 ms. Subjects were asked to indicate in which interval the Glass pattern was presented, and whether the Glass pattern was radial or concentric. In the trial shown, a radial Glass pattern is presented in the second interval. (B) Adaptation experiment: In these experiments, a 5-s top-up adaptation preceded the presentation of the test stimuli. Subjects were initially exposed at the start of each session to the adaptation pattern for 2 min. In the trial shown, the adaptation pattern is a green (azimuth 180) radial pattern. A red (azimuth 0) concentric Glass pattern is shown in the second interval.

thresholds for the detection of randomly oriented dot pairs in several directions of color space. The number of sessions that each subject ran depended on the subsequent experiments they would participate in. In total, there could be six different directions tested, along the three axes of the DKL color space.

In a two-interval forced-choice procedure, subjects were presented with an array of randomly oriented dot pairs on a uniform gray field, or a uniform gray field alone in a random order. Subjects had to indicate in which interval the array of random dots was presented. The array's color or luminance amplitude varied according to the staircase protocol described in the previous section. Distinct auditory feedback indicated correct and incorrect judgments.

The color or luminance intensity of the stimuli generated in the subsequent experiments was calculated from the data obtained in this experiment. For each subject, each DKL direction was individually scaled in terms of multiples of detection thresholds. All colors and luminance presented in subsequent experiments were thus at equal multiple of thresholds, which was chosen to be the maximal achievable on our equipment for each subject.

In the first, baseline experiment, we measured each subject's threshold for the detection of concentric and radial Glass patterns without adaptation. The procedure was identical to the one described in the Experimental procedure section, except that the initial and top-up adaptations were omitted.

Experiment 1 examined the effect of adaptation to color and form on the detection of colored Glass patterns. The adapting stimulus was either a concentric or radial Glass pattern isoluminant with the background with an azimuth of 0° (red), 90° (yellow), 180° (green), or 270° (blue). The adapting Glass patterns had 100% coherence. For a given adapting stimulus, we measured each subject's sensitivity to both concentric and radial colored Glass patterns with azimuths of 0°, 90°, 180°, and 270°. It took four different sessions to get the coherence thresholds for all eight test conditions for a given adapting stimulus. Eight subjects participated in this experiment.

Experiment 2 examined the effect of adaptation to color and form on the detection of luminance Glass patterns. The adapting stimulus was a concentric Glass pattern isoluminant to the background with an azimuth of 0° (red), 90° (yellow), 180° (green), or 270° (blue). The test stimuli varied in luminance but not in chromaticity with the background. For a given adapting stimulus, we measured subject's sensitivity to both concentric and radial Glass patterns with elevations of 90° (bright dots on the gray background) and −90° (dark dots). It took two sessions to get the coherence thresholds for all four test conditions for a given adapting stimulus. A total of four subjects participated in this experiment.

Experiment 3 examined the effect of adaptation to luminance and form on the detection of colored Glass patterns. The adapting stimulus was a concentric pattern that varied with the background only in luminance with an elevation of either 90° or −90°. The characteristics of the test stimuli were the same as in Experiment 1. A total of three subjects were tested in this experiment.

Experiment 4 examined the effect of adaptation to luminance and form on the detection of luminance Glass patterns. The adapting stimulus was either a radial or concentric pattern that varied with the background only in luminance, with an elevation of either 90° or −90°. The characteristics of the test stimuli were the same as in Experiment 2. Five subjects were tested in this experiment.

Statistical analysis

To assess the significance of the different adaptation effects, we used analysis of variance (ANOVA) techniques. Unless otherwise specified in the Results section, we applied a two-way ANOVA with condition (adaptation and baseline thresholds) and color direction (or luminance polarity) of the test stimuli as factors to assess whether adaptation and baseline thresholds are statistically significant. Furthermore, we used a one-way ANOVA to evaluate whether a set of coherence thresholds varied significantly from each other. We used anova1.m, anova2.m, and multcompare.m functions in Matlab for our statistical analysis. For the analysis of the data in Figure 9, we used the Statistica software. We considered an effect significant whenever the p-value was less than 0.05. In our analysis of the preliminary experiments, we contrasted radial versus concentric baseline results.

Results

Preliminary experiment

The axes of DKL space were scaled individually for each subject. Across subjects, the multiple of detection thresholds ranged from 2.3474 to 5.0000 (mean = 3.9418, standard deviation = 0.7839). These values ensured that each stimulus is clearly visible and equally salient within subjects.

Baseline experiment

The results of the baseline experiments (without adaptation) served as reference sensitivity measures for subsequent experiments. Results from the baseline experiments are shown in Figure 2. The average coherence thresholds across 10 subjects for colored Glass patterns (dots isoluminant with the background plane) are shown in Figure 2A. Each of the 10 subjects was tested in the

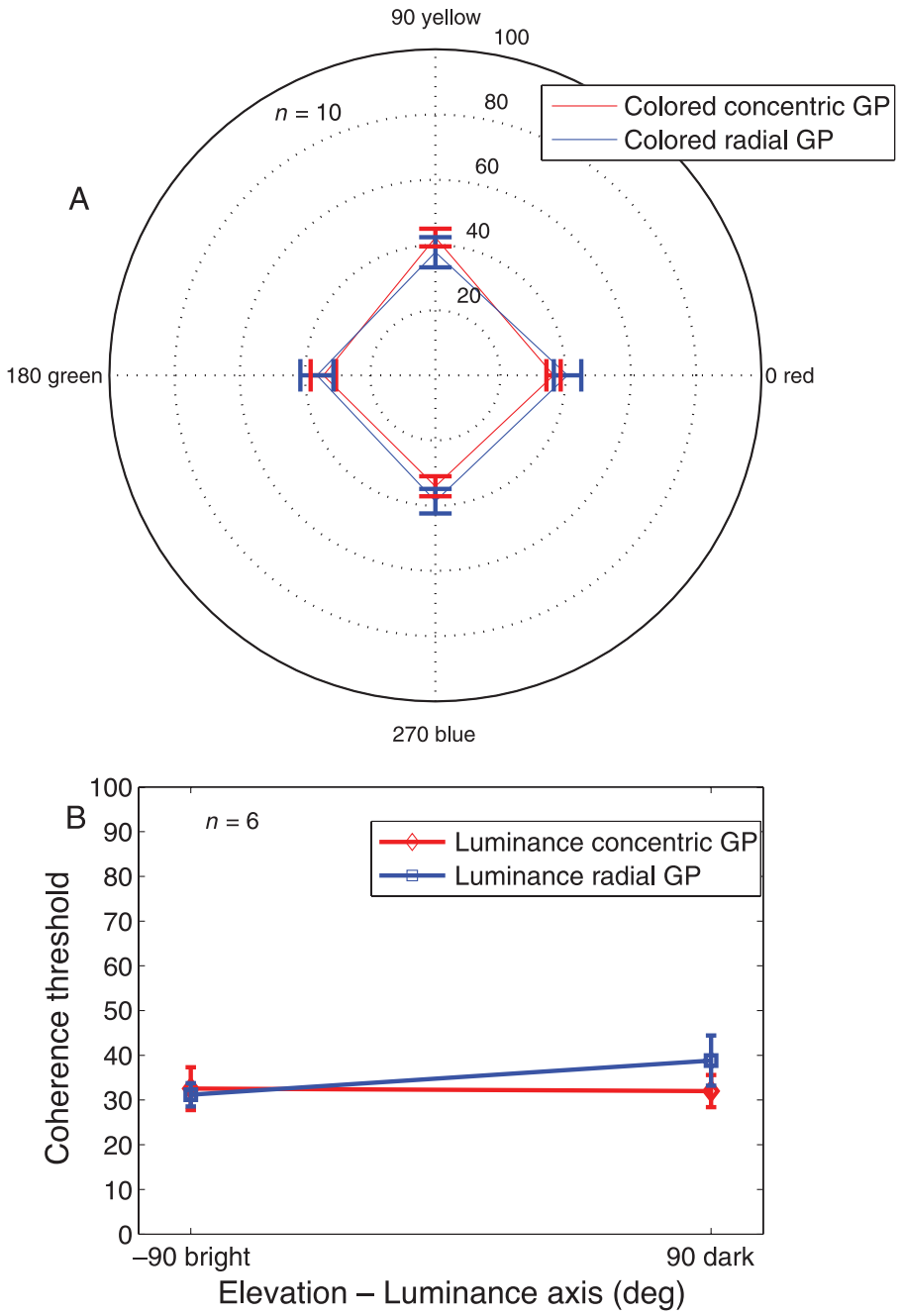


Figure 2. Baseline coherence thresholds for radial and concentric Glass patterns. (A) Baseline coherence thresholds as a function of dot azimuth in the isoluminant plane. (B) Baseline coherence thresholds as a function of added luminance contrast represented by elevation in the DKL color space. Error bars for this and subsequent figures represent the standard error of the mean (*SEM*).

four cardinal directions of DKL space. Figure 2B shows the coherence thresholds averaged across 6 subjects for luminance-based Glass patterns (dots along the luminance axis, orthogonal to the isoluminant plane). There are two possible directions subjects can be tested on: above (elevation = 90°) or below (elevation = −90°) the isoluminant plane.

In both cases, we found no significant difference in performance for Glass patterns that are comprised of dots with different colors ($F(3,36) = 1.58$, $P = 0.212$ for concentric Glass patterns; $F(3,36) = 0.16$, $P = 0.925$ for radial Glass patterns) or luminance polarities ($F(1,10) = 0.01$, $P = 0.9273$ for concentric Glass patterns; $F(1,10) = 1.54$, $P = 0.243$ for radial Glass patterns), or between radial and concentric Glass patterns ($F(1,72) = 0.34$, $P = 0.559$ for colored Glass patterns; $F(1,20) = 0.41$, $P = 0.5316$ for luminance Glass patterns). Previous psychophysical experiments had indicated a slight bias in the perception of concentric structure (Wilson & Wilkinson, 1998); in our case, this tendency was not significant.

Experiment 1

Experiment 1 explored whether there are mechanisms that are simultaneously selective for the form and color of Glass patterns. If that were the case, adaptation to a colored Glass pattern should elevate the thresholds for the detection of Glass patterns with the same (or similar) form and (similar) color but should leave the coherence thresholds for other patterns unaffected. If however the detecting mechanism is form selective but color invariant, then adaptation to a colored Glass pattern should elevate thresholds for the detection of Glass patterns with the same form irrespective of their color.

Figure 3 shows the percentage change in coherence thresholds compared to baseline (no adaptation) as a function of the dots' color for concentric and radial test patterns. Each polar plot shows the effect of adaptation of either a concentric or radial colored Glass pattern.

In each polar plot, the angle indicates the color of the test pattern and the magnitude indicates the percent change from the baseline measures. The solid circle in the center of each plot represents zero percent change from baseline. Threshold decreases compared to baseline after adaptation are thus plotted within this circle (negative percentage change) and threshold increases without. The threshold's percent change for the detection of concentric patterns is shown in red, those for radial in green. The arrow in each graph indicates the color of the adapting stimulus. The first column (panels (A)–(D)) shows the results after adaptation to concentric Glass patterns and the second column (panels (E)–(H)) after adaptation to radial Glass patterns.

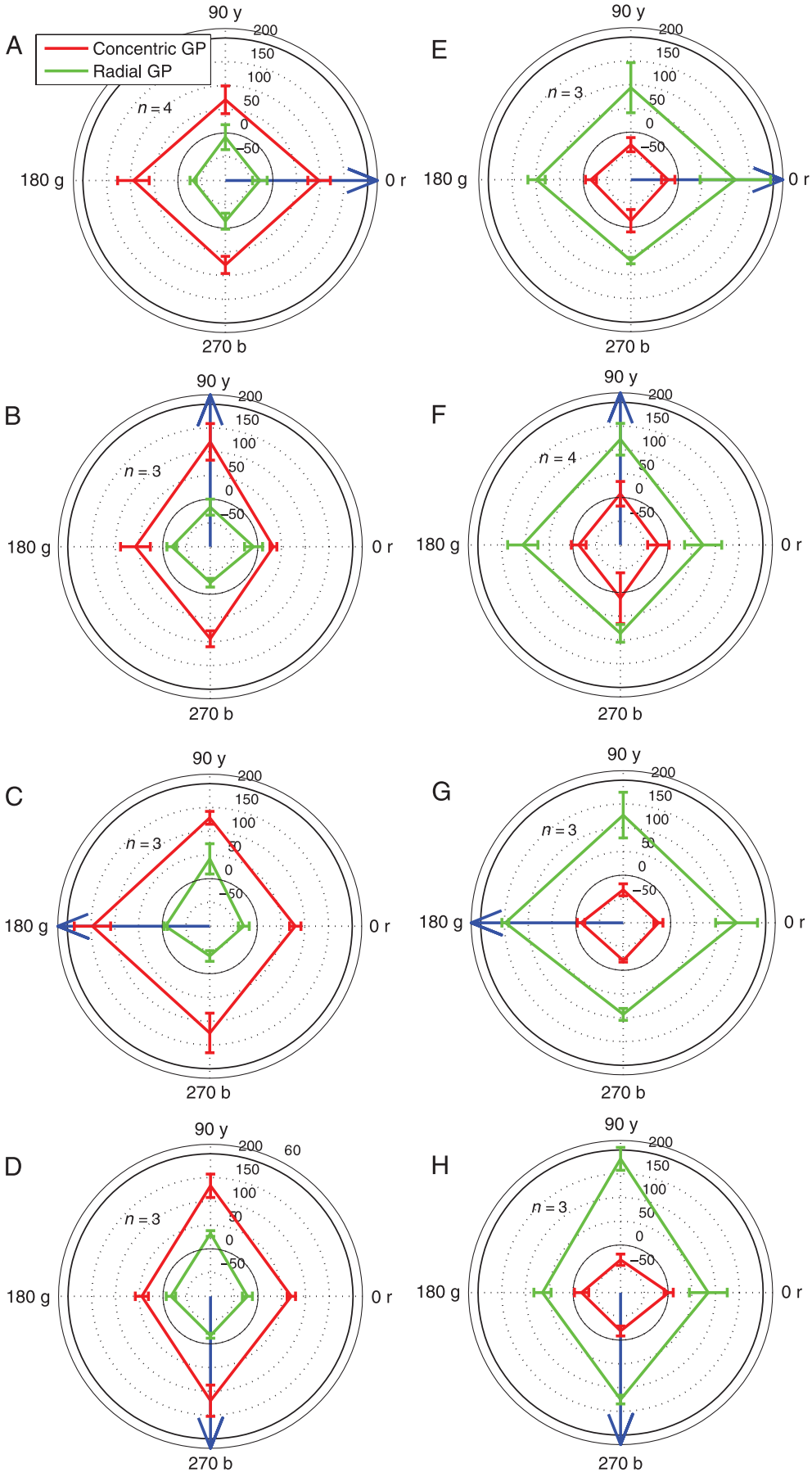
Several aspects of the data should be noted. First, it is immediately apparent that there is a significant elevation of coherence thresholds when adapting and test stimuli have the same form irrespective of their color. Indeed, we found that whenever adapting and test stimuli had the same form, the difference in coherence between baseline and adaptation data was statistically significant (two-way ANOVA, $29.21 < F(1,16) < 101.51$, $P < 0.0001$).

Second, the data show a consistent decrease in threshold when adapting and test patterns have different forms. This effect is statistically significant (two-way ANOVA, $5.83 < F(1,16) < 8.83$, $P < 0.05$) in three of the eight conditions. We interpret this result in light of the adaptation aftereffect reported by Clifford and Weston (2005). Adaptation to a concentric pattern induces subsequent random patterns to appear radial, and vice versa. Thus, in trials containing for example a radial pattern and a random one after adaptation to a concentric pattern, subjects are biased and perceive a radial pattern in both intervals. This tendency is visible in the analysis of errors made in these experiments: when subjects chose the wrong interval, they did not indicate seeing a radial or concentric pattern with equal probability (50%), as would be expected in the absence of aftereffect, but overwhelmingly (78% on average) indicated the pattern opposite to the adaptation pattern. Moreover, we compared the overall percentage of times subjects indicated one pattern type (radial or concentric) between the baseline and adaptation experiments. This gives us a quantitative estimate of the change in bias that subjects could have for one or the other pattern type. We determined using a two-way ANOVA (with factors azimuth difference and bias change versus coherence threshold change) whether the bias alone could explain the changes in coherence thresholds seen after adaptation. When adapting and test patterns have the same form, bias alone cannot explain the change in coherence threshold ($0.06 < F(1,96) < 0.12$, $P > 0.5$). Indeed, the change in coherence threshold in that case is 6.4 times higher than the change in bias. This shows that adaptation leads to a significant decrease of sensitivity for the same form. However, when adapting and test stimuli have different forms, the change in coherence threshold (i.e., decrease) is completely accounted for by the bias ($120.12 < F(1,96) < 121.84$, $P < 0.0001$).

Finally, it appears that although significant adaptation occurs in all cases when adapting and test stimuli had the same form, there is a tendency for the effect to be stronger when adapting and test patterns have the same color. In these graphs, some of the outer diamonds (red in panels (A)–(D), green in panels (E)–(H)) are slightly elongated in the direction of the adapting color (arrow). This color-specific adaptation is, however, not statistically significant (one-way ANOVA, $0.19 < F(3,8) < 3.51$ or $0.23 < F(3,12) < 0.92$ depending on the number of subjects for the condition, $P > 0.05$). Although we tried to minimize adaptation of the local filters coding the dot pairs' orientation by refreshing the adapting patterns every 500 ms (see Methods section), the present observation suggests that some adaptation of the local oriented filters might have occurred.

To ensure that our results are not affected by individual deviations from photometric isoluminance, two subjects ran the same experiments with smaller Glass patterns whose dots had been perceptually equated in luminance with the background (see Methods section). The results of these experiments are shown in Figure 4. The data for adaptation to concentric and radial patterns have been averaged to illustrate the effect of adaptation to the same or different form.

Figure 3. Results from Experiment 1: adaptation to colored Glass patterns. Percentage change from the baseline coherence thresholds as a function of color (azimuth in the isoluminant plane). The left column (A–D) shows results after adaptation to a concentric pattern, the right column (E–H) to a radial pattern. Each row shows adaptation to a specific color ((A) and (E): red, (B) and (F): yellow, (C) and (G): green, (D) and (H): blue). The solid circles at the center of each plot indicate 0 percent change compared to baseline. In each graph, the arrow indicates the color of the adapting stimulus. For each plot, *n* indicates the number of subjects.


A
Concentric GP
Radial GP
n = 4
B
n = 3
C
n = 3
D
n = 3
E
n = 3
F
n = 4
G
n = 3
H
n = 3
90 y
180 g
0 r
270 b
200
150
100
50
0
−50
60

In these plots, we observe the same pattern of results as in Figure 3. Most importantly, we see strong adaptation (two-way ANOVA, $8.22 < F(1,8) < 18$, $P < 0.02$) for test patterns having the same form as the adapting pattern, irrespective of their color, and a slight decrease in threshold for the opposite form. The latter effect is significant in only one out of eight conditions (two-way ANOVA, $F(1,8) = 8.34$, $P = 0.02$). Note that because of the reduced stimulus size, baseline thresholds were higher in this experiment, particularly for the concentric pattern. The higher baseline threshold explains why the adaptation effects are somewhat weaker in this experiment than those seen in Figure 3. Using perceptual rather than photometric isoluminance does not affect these two subjects' results and suggests that the whole group's results cannot be explained solely by artifacts due to individual variations in isoluminance points.

To further investigate whether color has any influence on the degree of adaptation in this experiment, we grouped our results depending on the color difference (i.e., difference in azimuth) between adapting and test stimuli. We divided our data into two groups: one where adapting and test stimuli had the same form and the other where adapting and test stimuli had different forms. Figure 5 shows the percentage change from the baseline as a function of azimuth difference between the adapting and test stimuli. In Figure 5A, adapting and test stimuli have the same form; in Figure 5B, they have different forms.

In both cases, we ran a one-way ANOVA for radial and concentric adapting patterns and found no significant difference for different azimuth differences ($1.75 < F(3,48) < 2.44$ $P > 0.05$). Note that when both the adapting and test stimuli were concentric the P-value was close to our significance level ($P = 0.076$) suggesting that there is a slight effect of azimuth difference. This tendency can be attributed to local adaptation, as explained above.

Together, these results indicate that: (1) adaptation to a colored Glass pattern elevates the coherence thresholds for the perception of subsequent Glass patterns of the same form irrespective of their color, (2) adaptation to a colored Glass pattern tends to decrease thresholds for subsequent patterns of the opposite form irrespective of their color, and (3) the degree of adaptation is independent of the azimuth difference between adapting and test stimuli. These results thus indicate that global form mechanisms are color invariant.

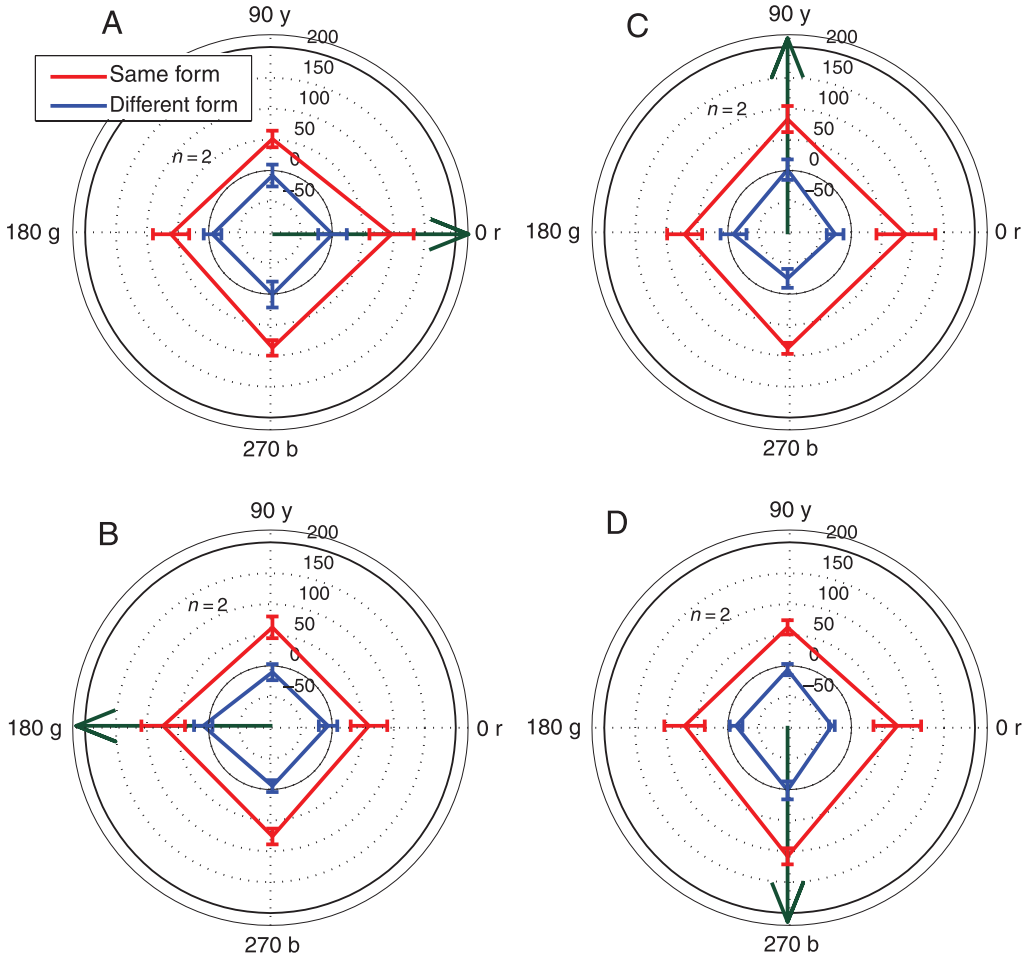


Figure 4. Effects of adaptation to colored Glass patterns on the detection of colored Glass patterns for stimuli at perceptual isoluminance. Red data are for adapting and test stimuli of the same form, blue of different form. Other conventions as in Figure 3.

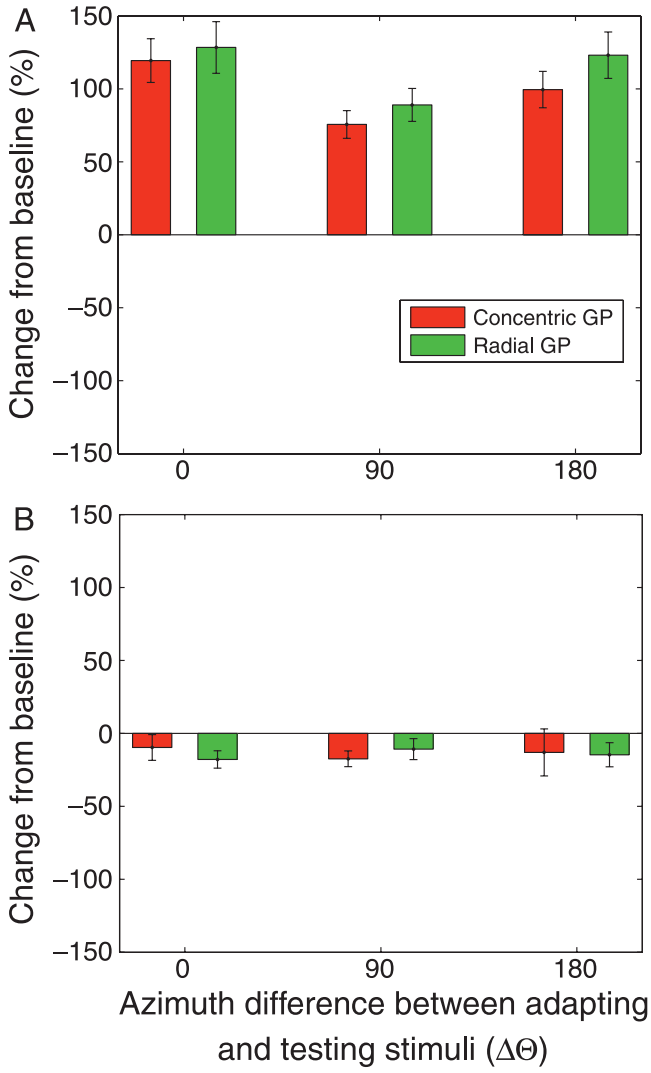


Figure 5. Percentage change from the baseline coherence thresholds as a function of azimuth difference between adapting and test stimuli for 10 subjects. (A) Both adapting and test stimuli have the same form. (B) Adapting and test stimuli have different form.

Experiment 2

Our results from Experiment 1 support the idea that mechanisms responsible for Glass pattern perception are color invariant. In Experiment 2, we tested the effect of colored concentric Glass pattern adaptation on luminance Glass patterns. The results of Experiment 2 are shown in Figure 6. Figures 6A–6D show the percentage change of coherence thresholds compared to baseline as a function of luminance polarity for concentric and radial test Glass patterns. Each plot shows results for adaptation to one color.

When both adapting and test stimuli were concentric, there is a statistically significant decrease in performance in three out of four conditions (two-way ANOVA, $16.65 < F(1,8) < 96.69$, $P < 0.005$). The fourth condition was close to significance ($F(1,8) = 5.01$, $P = 0.055$) Furthermore, there is no statistically significant difference in the degree of adaptation for different combinations of color and luminance on the adapting and test patterns when both adapting and test stimuli were concentric or when the test stimulus was radial. When adapting and test stimuli were of different form (i.e., when the test pattern was a radial Glass pattern), coherence thresholds are statistically different from the baseline thresholds for two out of four conditions (ANOVA, $8.04 < F(1,8) < 8.77$, $P < 0.05$).

We used again perceptually isoluminant adapting stimuli to rule out any luminance artifacts. Our results are similar to those described in the previous paragraph (statistically significant difference in three out of four conditions when both adapting and test stimuli are concentric), the only difference being that the difference between baseline and adapting stimuli never reached significance when the adapting and test stimuli had different form.

Experiment 3

Given the results of Experiment 2, it is natural to ask whether luminance Glass patterns can modulate the perception of colored Glass patterns. We thus tested the effect of adaptation to luminance concentric Glass patterns on the perception of colored Glass patterns. The results of this experiment are shown in Figure 7. Coherence thresholds of colored concentric Glass patterns are elevated irrespective of the luminance polarity of the adapting concentric patterns (two-way ANOVA, $78.1 < F(1,16) < 105.29$, $P < 0.0001$). There is no difference in the degree of adaptation when the adapting and test stimuli were concentric or when the test stimulus was radial (one-way ANOVA, $0.14 < F(3,8) < 0.57$, $P > 0.5$). The increase in sensitivity to the opposite form, in this case, is not statistically significant for any of the two conditions (two-way ANOVA, $0.03 < F(1,16) < 0.25$, $P > 0.5$).

As in the previous two experiments, we also used perceptually isoluminant adapting patterns and got the exact same statistical trends described for the photometrically isoluminant stimuli.

Experiment 4

Finally, in Experiment 4 both the adapting and test stimuli were luminance Glass patterns. The results of Experiment 4 are shown in Figure 8. The coherence thresholds were still raised when both the adapting and test stimuli were of the same form irrespective of their luminance polarity.

The increase in coherence thresholds when both the adapting and test stimuli were the same reached significance

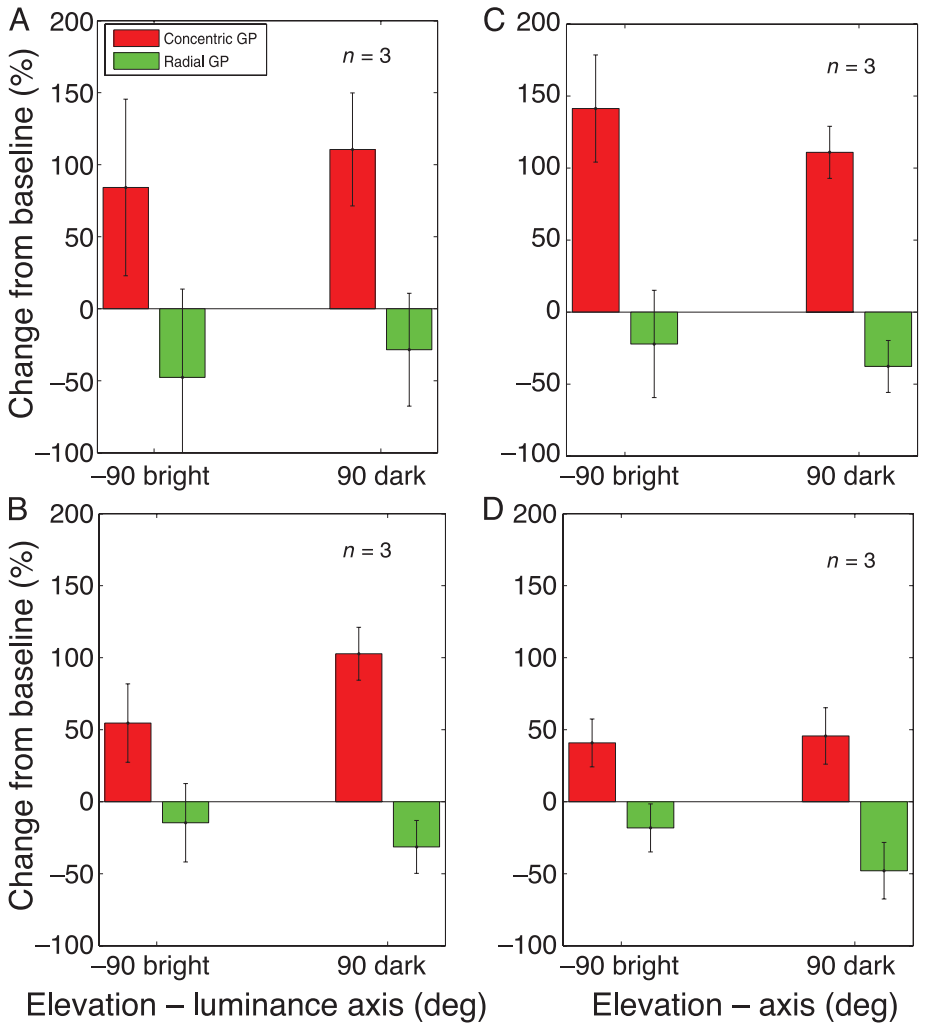


Figure 6. Results from Experiment 2. Percentage change from the baseline coherence thresholds as a function of added luminance contrast (represented by elevation in the DKL color space). In all cases, the adapting pattern was concentric. Each plot shows results for adaptation to a different color ((A) red, (B) yellow, (C) green, (D) blue).

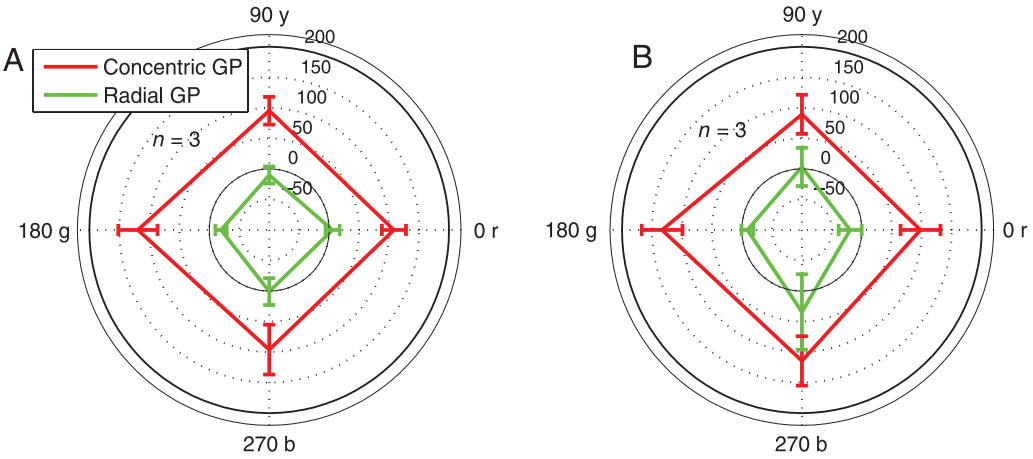


Figure 7. Results from Experiment 3. Percentage change from the baseline coherence thresholds as a function of color after adaptation to luminance patterns. In all cases, the adapting pattern was concentric. Each plot shows results for adaptation to a different luminance polarity ((A) bright, (B) dark). Other conventions as in Figure 3.

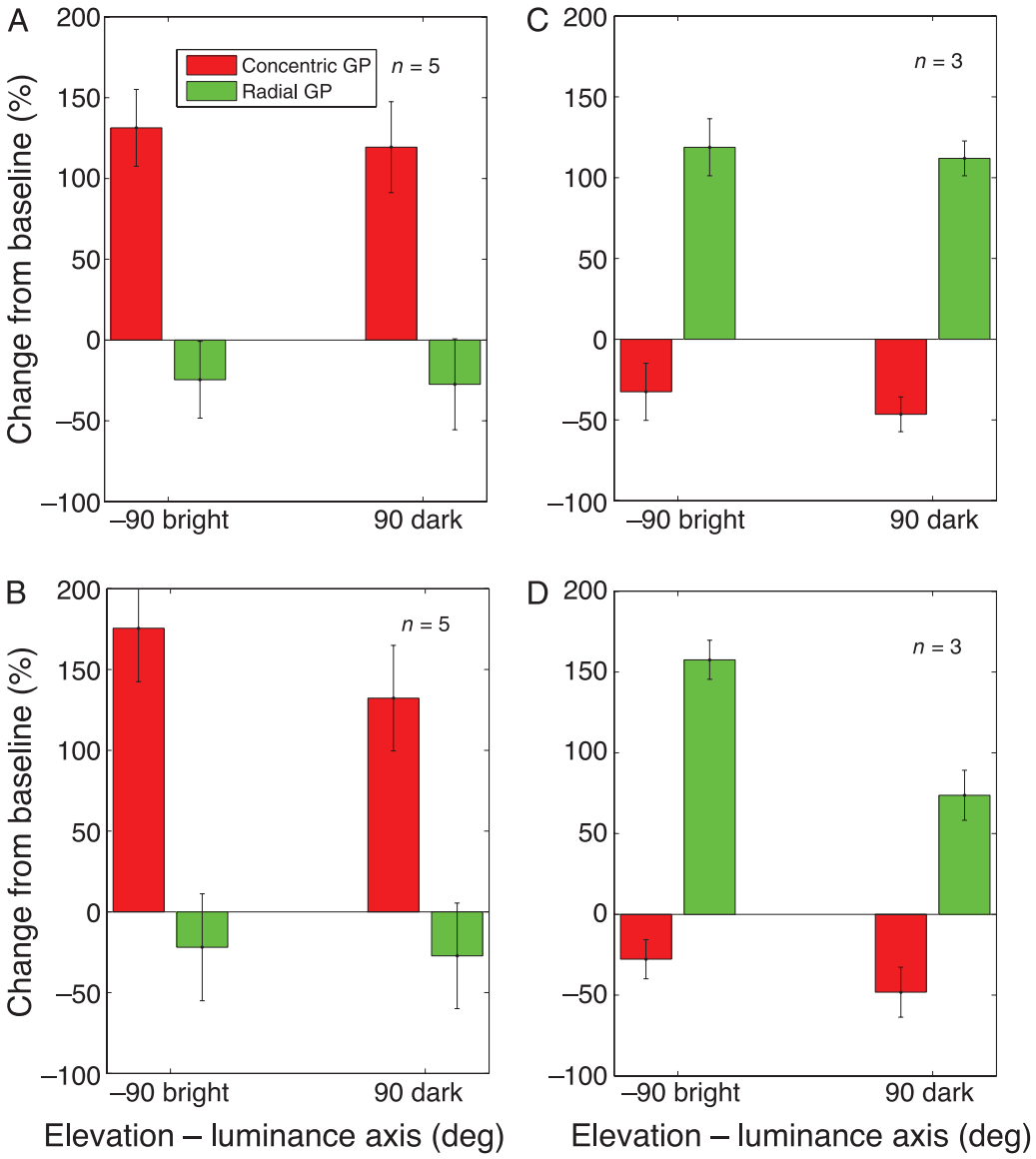


Figure 8. Results from Experiment 4. Percentage change from the baseline coherence thresholds as a function of luminance polarity after adaptation to luminance patterns. Each plot shows results for adaptation to a different form and luminance polarity ((A) bright concentric, (B) dark concentric, (C) bright radial, and (D) dark radial).

in all cases (two-way ANOVA, $80.53 < F(1,16) < 119.28$, $P < 0.0001$ for concentric and $22.89 < F(1,8) < 52.13$, $P < 0.005$ for radial patterns). When the adapting and test stimuli had different forms, there was a statistically significant decrease in coherence thresholds (two-way ANOVA, $7.18 < F(1,16) < 7.42$, $P < 0.05$ for concentric and $6.04 < F(1,8) < 8.76$, $P < 0.05$ for radial adaptation). Finally, there was no statistically significant deviation in the degree of adaptation for any combination of adapting and test stimuli (one-way ANOVA, $0.02 < F(1,4) < 5.02$, $P > 0.05$).

Our main results are summarized in Figure 9, which plots the averaged percentage change in coherence thresholds for all conditions.

This figure shows that, in all cases, adaptation to either concentric or radial patterns led to significant threshold increases for the same form. The threshold elevations, however, are not always of the same magnitude (ANOVA, $F(5, 114) = 3.5911$, $P = 0.004$). Two factors contribute to these differences. First, as noted above, the tendency for adaptation to be stronger for the same compared to different colors (discussed in the results of Experiment 1) is illustrated here by the difference in height between the red positive columns. The same tendency is seen for luminance polarity in the gray columns. It is likely due, in that case as well, to adaptation of the local, oriented filters in addition to that of the global form mechanism. Second, these differences could reveal different degrees of

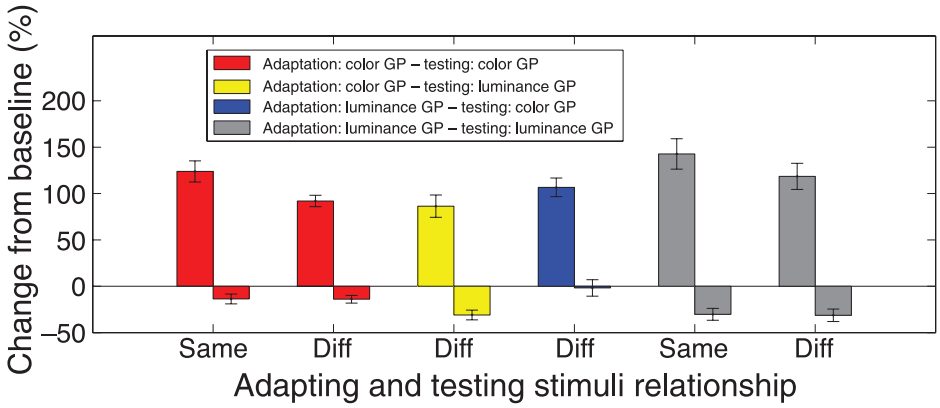


Figure 9. Percentage change from baseline coherence thresholds for all conditions. The positive columns show test coherence threshold elevations following adaptation to the same form. The negative columns show threshold decreases following adaptation to a different form. The red bars indicate the effect of color adaptation on colored patterns; the yellow bars indicate the effect of color adaptation on luminance patterns; the blue bars indicate the effect of luminance adaptation on colored patterns; and the gray bars indicate the effect of luminance adaptation on luminance patterns. The "same" label under the red bar indicates the thresholds when adapting and test stimuli have the same color, the "diff" when they have different colors. The "same"/"diff" labels under the gray bars indicate thresholds when adapting and test stimuli have the same/different luminance.

adaptation between the luminance and color adaptation conditions. Indeed, the gray and blue columns appear higher than the corresponding red and yellow ones, suggesting that luminance adaptation yields stronger threshold elevation than color adaptation. When compared directly, the difference in adaptation to luminance compared to adaptation to color does indeed reach statistical significance (one-way ANOVA, $F(1,182) = 6.2183$, $P = 0.0131$). This analysis thus shows that global form mechanisms are invariant to color and luminance in the sense that they can be adapted by both but may be differentially affected by these two attributes. Finally, Figure 9 also illustrates consistent threshold decreases following adaptation to a different form. As discussed with the results of Experiment 1, this effect can be explained by the bias for the opposite form induced by adaptation to either concentric or radial pattern and is not likely to reflect a true change in sensitivity. In that case, there is no statistically significant difference between adaptation to luminance compared to color (negative blue and gray columns compared to red and yellow ones, one-way ANOVA, $F(1,182) = 0.0489$, $P = 0.8252$).

Discussion

We used adaptation to investigate the effect of color and luminance on global form-selective mechanisms. Our results provide evidence for invariance to color and luminance polarity in the early stages of global form processing.

The results from Experiment 1 contradict the earlier report that Glass pattern mechanisms are broadly selective for color (Cardinal & Kiper, 2003). To determine the color bandwidth of global form mechanisms, Cardinal and Kiper embedded Glass pattern in random noise dots and varied the chromatic content of signal and noise independently. They found that thresholds for the detection of concentric Glass patterns depended on the pattern and noise colors, with thresholds being highest when the azimuths of signal and noise were the same or similar. They interpreted this result as a given mechanism's tuning in color space. The present study leads us to propose an alternative explanation for these earlier results. Threshold elevation in Cardinal and Kiper's study could be due to false pairings between signal and noise dot pairs. Pairing of Glass pattern dots into dipoles is performed by local mechanisms that are known to be color selective (Mandelli & Kiper, 2005; Wilson & Switkes, 2005) Thus, signal and noise dots will be more likely to form false pairings (i.e., dipoles with the wrong orientation) when their color is similar than when it is different. The occurrence of these false pairings essentially reduces the pattern's coherence and leads to a detection threshold elevation. This explanation is supported by the observation that multicolored Glass patterns (in which each dipole has a color randomly selected in color space) are more easily detected than uniformly colored Glass patterns in which false pairings are more likely to occur (Grimm, Rentzeperis, & Kiper, unpublished results). The present results are thus in agreement with those of Wilson and Switkes (2005) and show that Glass pattern mechanisms are not color selective.

Our results show that the degree of adaptation to a specific form is largely independent of the color similarity between adaptation and test patterns, although we do see a slightly larger increase in threshold when adapting and test patterns have the same color. That this effect is weak is somewhat surprising considering that when their colors are the same, both the local and global form mechanisms

should adapt, while only the global form mechanism should adapt when their colors are different. This suggests that adaptation mostly occurs at the global stage. It is possible that the test pattern was processed by local mechanisms that had not been stimulated during the adaptation period, or that the periodical changes in dipoles' position during adaptation (see Methods section) greatly reduced adaptation of the local mechanisms. Since adaptation of local, orientation-selective mechanisms is well documented (Engel, 2005; Wade & Wandell, 2002), we favor the second interpretation.

Our results show that adaptation to luminance produces stronger effects than adaptation to color. Since our adapting stimuli were equated for visibility, we do not have a clear explanation for this result. One possibility is that equating stimuli in multiples of detection threshold is not the correct metric to compare the strength of adaptation across conditions. For example, it is known that RMS cone contrast of luminance-defined stimuli is considerably higher than that of isoluminant red or green stimuli at detection threshold (Chaparro, Stromeyer, Kronauer, & Eskew, 1994). If strength of adaptation in our experiment is proportional to RMS cone contrast, we would thus expect to see a difference between adaptation to luminance and color. Future experiments using stimuli equated in terms of RMS cone contrasts will shed more light on this issue.

Our results with luminance patterns are at odds, with those of Badcock, Clifford, and Khuu (2005) and some of the results of Wilson et al. (2004), who concluded from their results that contrast polarity pathways are segregated at the global stage of processing. Their experiment measured thresholds for the detection of Glass patterns embedded in noise of the same or different contrast polarity. They found higher thresholds for the same compared to opposite polarity. We propose that their results can be explained by false pairings due to the selectivity of the local orientation mechanisms, just as for Cardinal and Kiper's (2003) study mentioned above.

These and previous results suggest that the cortical processing of colored, global form might proceed in several stages. First, local orientation, but not global form, signals are processed by orientation-selective neurons in early visual cortex (Smith et al., 2002, 2007). Many V1 and V2 neurons are known to be simultaneously orientation and color selective (see Gegenfurtner & Kiper, 2003 for a review). These chromatic and orientation signals are then pooled over space to generate a percept of global form. This is likely to occur in area V4, known to contain neurons selective for complex shapes (Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996). Since neurons in posterior V4 are also known to be often color selective (Schein & Desimone, 1990), and since posterior V4 cells with simultaneous color and complex form selectivity have been reported (Kiper, 2005), it is likely that the initial integration of local signals is done by posterior V4 neurons that retain a broad color selectivity. The outputs of these neurons could then be passed to more anterior neural populations (in anterior parts of V4, or in inferotemporal cortex) that pool information across all directions of color space. A recent study comparing the processes involved in the detection and identification of global form patterns (Seymour, McDonald, & Clifford, 2009) suggested that visual features such as contrast polarity must be bound to the form percept by mechanisms located beyond the form detection stage. It is possibly the activity of these color- and luminance-invariant mechanisms that is revealed by the experiments presented here.

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